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Theoretical and analytical advances in mammalian isotope ecology: an introduction

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In this introductory paper we describe the 10 papers that compose this Special Feature *Theoretical and analytical advances in mammalian isotope ecology*. This Special Feature contains 6 review-style papers, written by some of the leaders in the field. These are followed by 4 data-driven articles. The review-style papers were presented at a symposium we organized during the 90th annual meeting of the American Society of Mammalogists. The symposium was dedicated to Donald M. Schell (1940–2009), who pioneered research in isotopic ecology.

Key words: diet, incorporation rate, migration, mixing models, natural abundance, stable isotopes

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The use of stable isotope analysis in the study of mammalian migration, diets, and body condition has dramatically increased in recent years (Fig. 1). Until recently, however, the publication pace of stable isotope studies in the *Journal of Mammalogy* has lagged. The use of stable isotope analysis allowed community and population ecologists, physiologists, paleobiologists, and those interested in animal behavior to gain valuable insights into questions that have been previously confounding. The recent interest among members of the American Society of Mammalogists in this relatively new and powerful technique prompted us to organize a special symposium entitled *Stable Isotopes in Mammalian Research* at the 90th annual meeting of the American Society of Mammalogists in Laramie, Wyoming, in June 2010. Our goal was to introduce the theoretical and analytical advances in stable isotope analysis to members of the American Society of Mammalogists. Therefore, we invited leaders in the field to contribute papers. The success of the symposium and interest in the topic motivated us to solicit articles from these contributors along with additional papers we believe will further our understanding of mammalian isotopic ecology.

The 1st manuscript of this Special Feature was written as a beginner's guide (Ben-David and Flaherty 2012). In that paper, the authors provide the background needed to understand the more advanced and theoretical papers that follow. It starts with explanation of the basic chemical and physical properties of isotopes and describes the principles of isotopic fractionation and discrimination. Following this general overview, the beginner's guide concentrates on applications to animal ecology, explaining the processes that govern isotopic incorporation into animal tissues, listing different applications, and providing some cautionary notes and caveats (Ben-David and Flaherty 2012). This 1st manuscript ends with insights into the future direction of the field.

The 2nd manuscript in this Special Feature is by Newsome et al. (2012) and uses isotopic data from California sea otters (*Enhydra lutris*) to illustrate the various statistical and quantitative approaches available to describing resource and habitat use of animals from individual to community levels. The authors report on advantages and potential pitfalls of different approaches, which they classify into 3 categories: IsoSpace, which is a bivariate representation of the isotopic variation on the landscape (or seascape) of all potential foods in relation to the consumer; mixing models, in which the proportional contribution of different food items to the diet of a consumer is estimated with linear models; and DietSpace, which measures the degree of dietary specialization for an individual consumer and groups of consumers (Newsome et al. 2012). The authors compare the results and conclusions derived from the 3 approaches and provide recommendations for the proper application of each.

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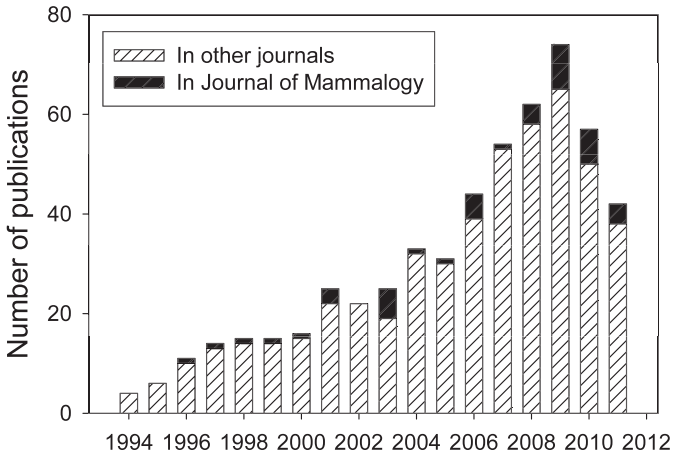


Fig. 1.—Number of published papers in which stable isotope analysis was used to determine migration, diet, niche, parasite–host interactions, or condition of mammalian species (hatched bars), excluding those that were published in the *Journal of Mammalogy* (black bars). For 2011, only papers published between January and September are included. Excluded are papers using mammalian model species in human medical applications, homonid evolution, and ecosystem studies. Data were collected from the online search engines Web of Knowledge (apps.webofknowledge.com/) and Academic Search Premier (web.ebscohost.com/) and the American Society of Mammalogists' Web page (www.mammalsociety.org/journal-mammalogy; accessed 27 October 2011).

This paper is followed by an overview of mixing models and their development from simple single-isotope linear mixing models (Phillips 2001, 2012) to complicated Bayesian-based multiple-source models (Moore and Semmens 2008; Parnell et al. 2010; Phillips 2012). The author clearly explains the terminology, basic assumptions, and the effects of variation in source isotopic values and discrimination factors on the conversion of isotope data to estimates of dietary contributions (Phillips 2012).

The 4th article, by Martínez del Rio and Carleton (2012), provides a thorough overview of the physiological processes that govern the incorporation of dietary nutrients into animal tissues. Understanding these processes, which determine incorporation rates and routing of nutrients to various tissues, is critical for correct use of the analytical methods described by Newsome et al. (2012) and Phillips (2012). The authors describe the mechanisms that affect incorporation rates and residence time of stable isotopes with advanced mathematical models and provide guidelines for the design of future controlled experiments that will test some of the predictions they offer (Martínez del Rio and Carleton 2012).

The 5th paper in the Special Feature describes the application of stable isotope analyses to animal migration studies (Wunder 2012). Similar to the preceding papers Wunder (2012) provides a brief overview of our current knowledge (a detailed overview can be found in Hobson and Wassenaar 2008) and describes the latest analytical developments for assigning individuals to specific geographic areas. Although most migration studies have used hydrogen stable isotopes, Wunder (2012) emphasizes general approaches, highlights potential caveats, and discusses the strengths and weaknesses of nominal, likelihood-based, and continuous-surface assignment approaches.

In the 6th paper, Clementz (2012) describes the use of stable isotopes in paleodietary and migration reconstruction studies. Because the volume of literature on these topics is overwhelming (including archeological and paleontological studies—see Koch 2007), the author provides a subset of examples, largely from mammalian studies. Most importantly, Clementz (2012) describes the biomineralization processes that result in isotopic variation in fossils, provides guidelines for proper sample processing, and discusses the use of calcium isotopes, which are rarely used in ecological studies of extant species. Similar to preceding contributors, Clementz (2012) suggests priorities for future research in the field.

The 6 review-style manuscripts are followed by 4 data-driven papers, which we believe add to our knowledge beyond that covered in the preceding papers. The 1st of these, by Cryan et al. (2012), is an example of the use of multiple isotopes (carbon, hydrogen, nitrogen, and sulfur) to assess individual and community-level resource use. Although the authors describe patterns in big brown bats (*Eptesicus fuscus*) their approach could be adopted in other studies. The authors observed wide population-level variation for all isotopes, which likely reflects the complexity of the bats' isoscape, their mobility and opportunistic feeding habits (Cryan et al. 2012). The following paper by Pauli et al. (2012) reports on the innovative use of enriched stable isotopes (carbon, hydrogen, and nitrogen) to mark individual marten (*Martes americana* and *M. caurina*) and track dispersal events of free-ranging animals. The authors describe the efficacy of this method for marking small and midsized mammals in systems where the natural abundance isoscape is insufficiently variable to reliably identify migrants.

The final 2 papers in this issue describe results of captive studies. The 1st explores the effects of dietary nutrient composition and mass changes (including the unknown effects of pregnancy and lactation) on isotopic incorporation and discrimination in American mink (*Neovison vison*). The authors illustrate the effects of the complex interaction of these 2 factors on the emergent isotopic signal and the potential implication for interpretation of field data (Ben-David et al. 2012). The 2nd describes the results of a study on brown bears (*Ursus arctos*) where nutrient use is inferred from breath isotope analyses (Whiteman et al. 2012). The authors demonstrated that breath isotopic values rapidly tracked a dietary change, but that because CO_2 production and exhalation are influenced by nutritional state, additional measurements, such as respiratory exchange ratio, should be used to aid in interpretation of the isotope data (Whiteman et al. 2012). Because future mammalian research will likely require increased reliance on noninvasive sampling, understanding the advantages and limitations of interpreting breath isotope data are of fundamental importance.

Before delving into the series of papers, we—the contributors—would like to remember Donald M. Schell, to whom the symposium was dedicated. Don, a founding father of isotopic ecology, passed away in December 2009. During his career,

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Don conducted some of the pioneering research in isotopic ecology. He was the 1st to use stable isotopes to assess the feeding ecology of free-ranging whales (Best and Schell 1996; Schell et al. 1989), described migrations of whales using underlying differences in isotopic signatures of food webs in different oceans (Lee et al. 2005), illustrated the effects of anthropogenic CO_2 emissions on carbon isotope signatures (Schell 2001), and was one of the 1st to use compound-specific isotopic analyses to investigate animals diets. He was a mentor and an inspiration to those who now use this vital tool for ecological research.

Acknowledgments

We thank the editors of the *Journal of Mammalogy* for soliciting this Special Feature and the attendees of the special symposium on stable isotopes during the 90th annual conference who encouraged us to convert our presentations to articles. We also are thankful to all our colleagues who agreed to add to their busy schedules and write the papers presented here. Prior to submission, all manuscripts were internally reviewed by M. T. Clementz, E. A. Flaherty, L. A. Feliciti, H. J. Harlow, S. D. Newsome, J. N. Pauli, D. L. Phillips, J. D. Whiteman, N. Wolf, and M. Wunder.

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